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FISH SIZE, VISUAL RESOLUTION, AND PREY SELECTIVITY[1]

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Abstract. Planktivorous bluegill sunfish (*Lepomis macrochirus*) are known to consume large prey preferentially. Disagreement exists in the literature over whether this size-selectivity reflects optimal foraging behavior by the fish or relative prey encounter probability as predicted by a model in which apparent size of the prey determines foraging preference. As bluegills grow larger, their visual resolution increases, and this should affect prey choice under the apparent size model. In laboratory experiments, three sizes of fish were fed identical diets made up of three sizes of *Daphnia magna*. Large and medium-sized fish consumed relatively more large prey than predicted by the apparent size model, whereas the diet of small fish deviated only slightly from the apparent size model. For fish to be more selective than allowed by the apparent size model, they must be able to estimate absolute prey size. To do this requires good vision. Since diet selectivity was highly significantly correlated with the fishes' visual resolution in our experiments, we suggest that visual capability imposes a constraint on the ability of small bluegills to choose prey.

Key words: *apparent size;* Daphnia; *foraging strategies;* Lepomis; *predation; prey selection; size-selectivity; visual resolution.*

INTRODUCTION

There is widespread agreement that visually foraging planktivorous fish tend to consume zooplankton that are on average larger than the mean size present in their environment (see O'Brien 1979 and Zaret 1980 for reviews). There is much less agreement about the underlying causes of this "size-selective" predation. Brooks and Dodson (1965) ascribed the selection to both the greater visibility and the greater energy content of larger prey. Their dual discussion of prey conspicuousness and predator energetics presaged a divergence of emphasis by investigators studying fish foraging behavior that continues to the present. Werner and Hall (1974) studying bluegill sunfish (*Lepomis macrochirus*) feeding on *Daphnia* in the laboratory, found that the fish showed increasing specialization on larger prey with increasing prey densities. They concluded that the bluegills' feeding pattern was consistent with an optimal foraging model in which the diet chosen maximized energy gained per unit time spent foraging. O'Brien et al. (1976) proposed an alternative model to explain size-selective planktivory in which a fish presented with a choice of prey items always pursues the one that appears the largest. The zooplankter selected may in fact be the largest, or it may be a smaller prey item that only appears large because it is near to the fish and so subtends a large visual angle at the predator's eye. O'Brien et al. (1976) found that the diets predicted by their "apparent size model" computer simulation agreed well with the diets observed for the sunfish by Werner and Hall (1974), and they proposed that in choosing the apparently largest prey the fish would reduce energy expenditures in foraging without reference to the variables in optimal foraging models of search time, handling time, and the energy content of prey.

In recent studies, Werner and his co-workers have extended their investigation of fish feeding to natural and seminatural bodies of water (Mittelbach 1981, 1983, Werner et al. 1983), finding a pattern of feeding largely consistent with optimal foraging theory. At the same time, O'Brien and his co-workers (Drenner et al. 1978, O'Brien 1979, Vinyard 1980, Luecke and O'Brien 1981, Schmidt and O'Brien 1982, Wright and O'Brien 1982, Wright et al. 1983) have extended their more mechanistic model of fish foraging to include how other aspects of the predator (shape of the visual field, spacing of gill rakers), the prey (pigmentation, swimming behavior, escape ability), and the environment (light levels, turbidity) affect prey selection. Wright and O'Brien (1984) found fish diets in natural environments to be consistent with the predictions of their mechanistic model of prey choice.

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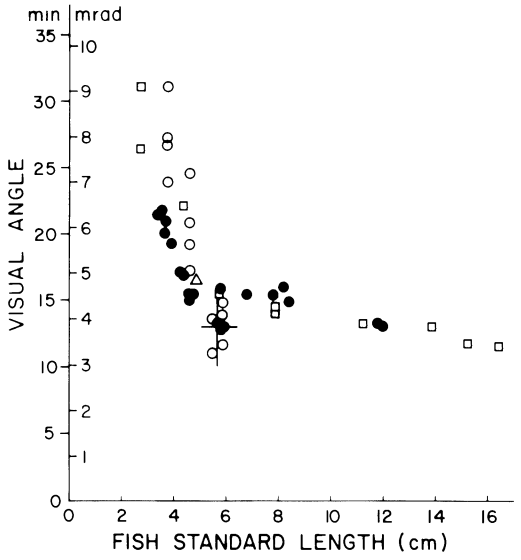

FIG. 1. Bluegill sunfish visual resolution as a function of fish body size. ○ mean reaction angles (minutes of arc or milliradians) from Hairston et al. (1982). □ mean reaction angles from data reported by Breck and Gitter (1983) multiplied by 0.64 (for reaction to mean prey diameter rather than to total length; from Hairston et al. 1982). △ mean reaction angle from data at high light density and low turbidity reported by Vinyard and O'Brien (1976); perpendicular lines represent range of data from Werner and Hall (1974) (in both cases, fish sizes were converted to standard lengths using a factor of 0.78 [from Beckman 1945], and *Daphnia* sizes were multiplied by 0.64 as described above). ● angular intercone spacing from histological sections, reported by Hairston et al. (1982) and from previously unpublished data, multiplied by 2 in accordance with Breck and Gitter (1983) and Helmholtz (1924).

Two investigators have undertaken laboratory studies in attempts to evaluate the accuracy of the apparent size model and optimal foraging theory as descriptors of the diet choice of fish feeding on *Daphnia*. Both Gibson (1980) and Gardner (1981) concluded that their data did not consistently support the predictions of the apparent size model of O'Brien et al. (1976) and that optimal foraging was the more likely explanation for their results.

Recently, however, the apparent size model computer simulation of O'Brien et al. (1976) has been shown to yield invalid predictions (Eggers 1982, Wetterer and Bishop 1985). Besides drawing into question the analysis by O'Brien et al. (1976) of Werner and Hall's (1974) experiment, reanalyses of Gibson's (1980) data by Wetterer and Bishop (1985) and Butler and Bence (1984) indicate that the diets of Gibson's fish were, in fact, consistent with the predictions of the apparent size model of foraging. At the same time, a lack of essential data on the reactive distances of fish at extremely high turbidity levels led Janssen (1983) and J. K. Wetterer (*personal observation*) to question Gardner's (1981) interpretation of his results.

The process of prey selection by visually foraging fish depends heavily on the visual capabilities of the predator, which affect its ability to detect and recognize potential prey. Neuroanatomical evidence has existed for a number of years suggesting that as fish grow larger, visual resolution increases (Müller 1952, Tamura 1957, Johns and Easter 1977). Behavioral studies also indicate better vision in larger fish (Baerends et al. 1960, Schmidt and O'Brien 1982). Hairston et al. (1982) found, for bluegill sunfish, that decreases in minimum separable visual angle with increasing fish size, measured as the spacing of retinal cells, were closely paralleled by decreases in the minimum angle calculated from the distance at which fish attacked prey of known size. Breck and Gitter (1983) showed, for bluegills, that the increase in visual resolution with fish size was curvilinear. The greatest change with growth occurred in small fish, and the change diminished in larger fish. Plotting these two data sets together (Fig. 1) shows a consistent pattern between studies. Other data for bluegills taken from Werner and Hall (1974) and Vinyard and O'Brien (1976) also fit this picture.

Hairston et al. (1982) and Breck and Gitter (1983) pointed out that if large fish have greater visual resolution than small fish, they will search a larger volume of their environment for prey at any one time. This fact presents an opportunity for testing whether the apparent size model is sufficient to describe diet choice by bluegill sunfish, or if it is necessary to invoke an explanation, such as optimal foraging theory, that permits greater selectivity (Gibson 1983). Wetterer and Bishop (1985) have shown that, except at extremely low prey densities, the apparent size model predicts virtually no change in foraging selectivity with changes in visual resolution. Butler and Bence (1984) reached a similar conclusion. On the other hand, vision is an important variable in optimal foraging models through its influence on the time spent searching for prey (Werner and Hall 1974). As encounter rate increases, a predator may be expected to specialize increasingly on those prey giving the highest energy yields (Pyke et al. 1977, Mittelbach 1981). For a fish feeding on different sizes of *Daphnia,* all requiring similar handling times, this means increasing size-selectivity with increasing prey encounter.

Here we report the results of an experiment in which three sizes of bluegill sunfish were fed *Daphnia magna* under controlled laboratory conditions. The fish sizes used permit a comparison of the diets of fish that differ in visual resolution.

MATERIALS AND METHODS

Bluegill sunfish were seined from Secret Lake and Bellville Pond, North Kingstown, Rhode Island, and kept in 300-L stock tanks for a minimum of 2 mo prior to experimentation. During this period the fish were fed daily rations of frozen brine shrimp or frozen earthworms. The diet choice experiments were run on three size classes of fish: 3.8 ± 0.2 cm, 6.0 ± 0.3 cm, and

7.6 ± 0.3 cm (mean standard length [SL] ±1 SD). Three replicates were run for each size class, with five fish per replicate. The experiments were conducted in circular plastic wading pools 98 cm in diameter filled with 11 cm of water (total volume 83 L). The pools were lined with white plastic to provide a uniform background for feeding. Illumination came from warm white fluorescent lamps giving 0.58 W/m^2 at the water surface.

Laboratory cultured *Daphnia magna* were separated into three size classes for the feeding experiments: small, 1.16 ± 0.22 mm; medium, 1.65 ± 0.18 mm; and large, 2.01 ± 0.18 mm (mean total length ±1 SD). Separation was accomplished with a series of nylon mesh sieves. The sieves were stacked in order of mesh size, with the coarsest mesh at the top, and *Daphnia* were stimulated to swim down through the sieves by placing a red light, to which they are positively phototactic (Smith and Baylor 1953), at the bottom. The setup effected size-sorting without causing any physical damage to the *Daphnia* (Li 1982). The initial distribution of prey given to the fish consisted of 328 small, 229 medium, and 200 large individuals. This ratio was chosen, using calculations from the apparent size model simulation kindly supplied by W. J. O'Brien, in an attempt to make all three prey sizes equally "apparent" at the start of the feeding bouts. Although the data analysis we carried out made this unimportant, each replicate feeding trial was started with exactly this distribution of prey.

Dry masses for each size class of *Daphnia* were measured on replicate groups of 10 individuals. Each group was dried at 80°C for 24 h and weighed on a Cahn electrobalance.

The fish were placed in wading pools 1 wk prior to the experiment and fed frozen brine shrimp. They were not fed for the 24 h immediately preceding the experiment. Each experimental feeding lasted 2 min, after which the fish were dip-netted, placed on ice for a few minutes to minimize regurgitation, and preserved in cold Formalin. *Daphnia* were removed from the fish stomachs under a stereomicroscope, and measured to the nearest 0.05 mm with an ocular micrometer at 20× magnification. Prey not eaten in the experiment were collected on a 0.260-mm mesh net and preserved in Formalin, and subsamples were measured to assure internal consistency in the experiment.

The expected diets predicted by the apparent size model were calculated using the computer simulation described in Wetterer and Bishop (1985). The simulation takes into account the reaction distances of fish to prey of different sizes, the abundance and size distributions of prey, and the physical constraints of the experimental environment. Values for reaction distance were taken from Hairston et al. (1982) and Breck and Gitter (1983). Other parameters were taken directly from the experimental setup described above. Observed and expected diets were compared using the preference index proposed by Manly (1974) and Chesson (1978, 1983): $\alpha_i = (r_i/n_i) \div \sum_{j=1}^{m}(r_j/n_j)$. Typically, the index has been used to compare n_i, the proportion of prey type i available in the environment, with r_i, the proportion of prey type i present in the diet; however, here we use it to compare the diet consumed by the fish (r) with the diet predicted by computer simulation to be consumed by fish feeding according to the apparent size model (n). The method gives us a means of assessing the relative degree of selectivity of fish of different sizes in comparison to each other and to the apparent size model.

TABLE 1. The numbers and biomass of *Daphnia magna* consumed by three sizes of bluegill sunfish in triplicate feeding trials. Data are means ± 1 SD.

Fish size	Number eaten	Dry biomass eaten (μg)	Mean mass per *Daphnia* (μg)
Large	196.3 ± 26.0	13 500 ± 1900	68.9 ± 0.8
Medium	257.0 ± 13.1	17 800 ± 602	69.6 ± 4.2
Small	345.7 ± 20.3	17 700 ± 2310	51.1 ± 3.8

RESULTS

Fish size had a significant effect on the pattern of prey selection observed in the experiment (Fig. 2). A two-way ANOVA showed significant differences between treatments in both the number of prey consumed from each of the three *Daphnia* size-classes ($F_{2,18}$ = 307.0, $P < .001$) and in the total number of prey consumed ($F_{2,18}$ = 44.6, $P < .001$). More importantly, the interaction between fish size and prey size was significant ($F_{4,18}$ = 9.51, $P < .001$), indicating that size-selectivity differed with fish size and was greater for large fish than for small fish. It is not obvious why the small fish consumed more prey than did larger fish. The small fish appeared to be calmer and less easily frightened in the experimental pools, and so may have had effectively more time to feed than larger fish. In addition, room temperatures were 4°C warmer during the trials using small fish, so their activity level may have been greater. Although small fish ate significantly greater numbers of prey than did medium-sized fish (Table 1; t = 6.36, df = 4, $P < .01$) there was no difference between the two in biomass consumed, due to the greater size-selectivity of the medium-sized fish, and hence the greater mean mass per prey consumed (Table 1; t = 5.66, df = 4, $P < .01$). Mean biomasses of prey taken by medium and large fish did not differ; however, the total biomass consumed by the large fish was lower than that consumed by medium-sized fish (t = 3.74, df = 4, $P < .05$), because the larger fish ate fewer prey.

Comparisons of the predictions of the apparent size model and our experimental results are shown in Fig. 2. The distributions of diet among the three prey sizes were significantly different from the predictions of the

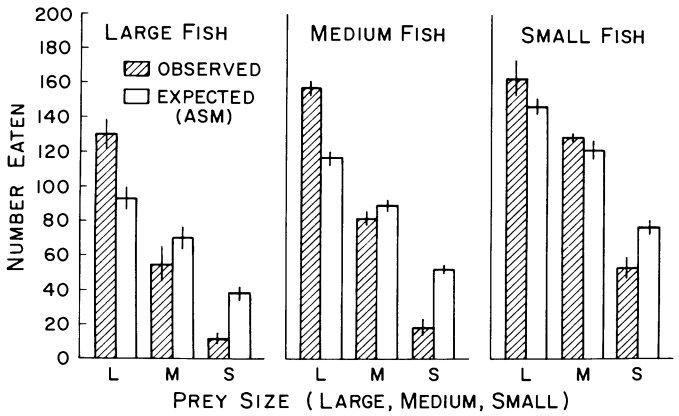

FIG. 2. Distribution of sizes of *Daphnia magna* consumed by small, medium, and large bluegill sunfish (Observed) in three replicate 2-min feeding trials, and the distribution predicted if the fish consumed the same number of prey according to the apparent size model (Expected). Bar heights are means (±1 SE).

apparent size model in all three replicate trials for the large fish and in all three replicate trials for the medium-sized fish (χ^2 values for the six comparisons ranged between 22.4 and 45.4, df = 2, $P \ll .001$). In each case the fish consumed more large *Daphnia* relative to medium-sized and small *Daphnia* than predicted. In the case of the small fish, diets differed from those predicted in two of the trials ($\chi^2 = 11.5$, df = 2, $P < .005$, and $\chi^2 = 17.7$, df = 2, $P < .001$) and were not significantly different from expectation in the third trial ($\chi^2 = 4.0$, df = 2, $P > .1$). Where the diets of small fish differed, they consumed more large and more medium-sized prey and fewer small *Daphnia* than expected. These results are summarized in preference values (α_i) comparing predator diet with computations from the apparent size model (Fig. 3). Large fish were the most selective and medium-sized fish were only slightly less selective. The small fish were distinctly less selective, with values much closer to those expected from the apparent size model.

DISCUSSION

We observed a regular pattern of increased selectivity with increasing fish size. The smallest fish, with the poorest visual resolution, were not significantly more selective or were only slightly more selective in their choice of prey than the diet predicted by the apparent size model. With increasing visual capability, medium and large fish showed a preference for larger prey that far exceeded expectation from the apparent size model.

The pattern is in striking conformity with the observations made by Werner et al. (1983) on the feeding of bluegill sunfish in a large experimental pond. Using a range of fish sizes comparable to that employed here, they found that small fish (3.55 cm SL) consumed a distribution of *Daphnia* sizes consistent with the apparent size hypothesis and less selective than that expected from the calculations of an optimal foraging model in 2 out of 2 comparisons. The diets of medium-sized fish (5.29 cm SL) differed from the predictions of the apparent size model in favor of taking larger prey in 2 out of 4 cases, and the diets of the large fish (7.30 cm SL) differed in 4 out of 4 cases. As in our experiments, Werner et al. (1983) observed that the fish showed a successive increase in selectivity with size, and that the difference in selectivity between the small and medium fish was greater than between the medium and large. They concluded that the trends in the fishes' diets were in qualitative agreement with their optimal foraging model.

Three variables in optimal foraging theory, as applied to bluegill sunfish, are functions of the predator's body size. As discussed in the Introduction, larger fish have enhanced visual resolution, which confers greater ability to detect prey and, hence, an increased prey encounter rate. This can be a very large effect. In a simple environment with dark *Daphnia* on a bright background, the reaction distance at which a prey item is sighted is linearly related to reaction angle. The volume searched for prey increases as the square (Eggers 1982) or the cube (O'Brien et al. 1976, Hairston et al. 1983) of reaction distance. Mittelbach (1981) calculated bluegill encounter rate with *Daphnia* as the number captured per unit time spent searching and found that it increased as the square of fish length; this function was used in his optimal foraging model (Mittelbach 1981, 1983) and that of Werner et al. (1983). The second variable dependent on fish size is prey handling time. For bluegills eating small *Daphnia,* handling time is close to 1 s regardless of fish size (Werner 1974, Mittelbach 1981). For larger *Daphnia,* handling becomes a function of prey length relative to the mouth gape of the fish, and so is greatest for small fish eating large prey. Using the regression equations from Werner (1974), handling times in our experiments ranged between 1.02 s (7.6-cm fish eating 1.16-mm prey) and 1.72 s (3.8-cm fish eating 2.01-mm prey), a measurable but not large effect. Finally, the metabolic rate of fish increases with body size, so the cost of searching and handling must also increase. Estimating metabolic rates

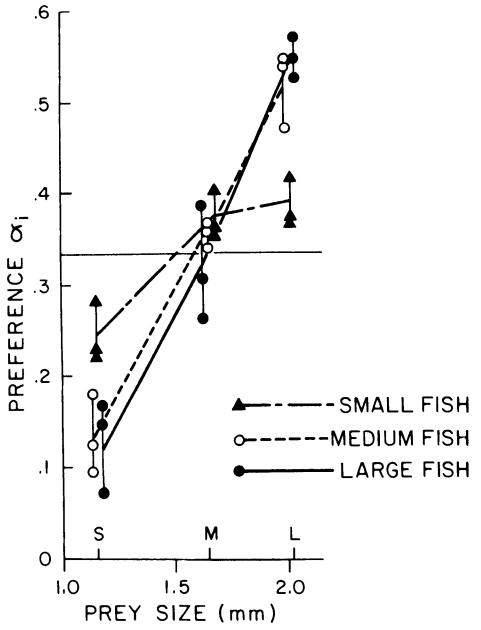

FIG. 3. Index of preference (α_i) by three sizes of bluegill sunfish for three sizes of *Daphnia magna* (small, medium, large). Here the index is used to compare the diet consumed by the fish with that predicted by the apparent size model. $\alpha_i = 0.333$ indicates perfect conformity. Only three prey sizes were offered; some data points have been displaced horizontally to facilitate illustration.

from regression equations given by Kesler (1978) and Wohlschlag and Juliano (1959) indicates that there may have been as much as a six-fold difference in metabolic rate between the small and large fish.

Optimal foraging theory predicts that the increased visual resolution in larger fish should lead to increased specialization on large *Daphnia*. Decreased handling time should have the same effect. Higher metabolic rates in larger fish may lead to specialization on large *Daphnia* if small prey represent a trivial energy increment in comparison to foraging costs. On the other hand, higher metabolism may lead more readily to hunger and hence to diet expansion. Including prey visibility, handling time, and fish metabolic rates in a specific model of bluegills foraging on *Daphnia*, Mittelbach (1981) and Werner et al. (1983) both predicted and observed increased diet specialization in larger fish. However, in both studies small fish were less selective in their diets than predicted by the optimization model. Unger and Lewis (1983) reported increased diet specialization of large over small individuals of an atherinid (*Xenomelaniris venezuele*) feeding on zooplankton in Lake Valencia, but they did not compare their results to the predictions of an optimal foraging model.

If search time plays a dominant role in the increased selectivity of larger fish, then we might expect there to be a statistical relationship between the prey preferences of fish of different sizes and their visual capabilities measured as reaction angles. For this example, reaction angle was estimated using the regression equation from a hyperbolic curve fit to the behavioral data of Hairston et al. (1982) and Breck and Gitter (1983) illustrated in Fig. 1 (Angle = 5.85 + [65.01/SL], where reaction angle is expressed in minutes of arc and SL in centimetres; with the angle expressed in milliradians, the equation is Angle = 1.7 + [18.9/SL]; $F_{1,22} = 61.0$, $P < .001$). Plotting preference values (α_i) for the large *Daphnia* against reaction angle for each of the three fish sizes (Fig. 4) revealed a highly significant negative relationship ($F_{1,7} = 49.9$, $P < .001$). Increased prey selectivity is a direct function of increased visual resolution (decreased visual angle). No such relationship existed for medium-sized prey ($F_{1,7} = 2.6$, $P > .1$), and a significant positive relationship was found for small prey ($F_{1,7} = 14.2$, $P < .01$). Thus, in our experiments, the amount by which the diet of bluegill sunfish deviated from the apparent size model is well predicted by the fishes' visual resolution.

An important distinction between the two models of prey choice discussed here is that the apparent size model both characterizes diet composition and provides a mechanistic description of how prey choice is made, while optimal foraging theory predicts optimal diet composition without reference to how, or whether, the predator is capable of making the appropriate selection. To feed according to the apparent size model, a fish need only consume the prey that occupy the greatest visual angle at the time of attack. However, when the diet includes more large prey than allowed by the apparent size model, as was the case in our experiments, the fish seemingly must be able to assess absolute prey size. There are several possible mechanisms that might enable a fish to achieve this, though none has experimental support as yet. First, bluegill sunfish have a small field of binocular vision directly in front of them, and if only prey within this field are considered, or if each prey item is independently brought into the field before a choice is made, then true prey size may be detected. As visual resolution grows with

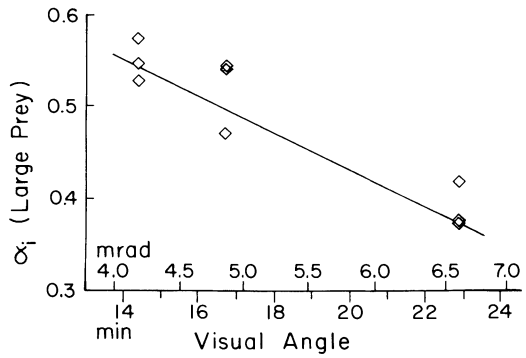

FIG. 4. Preference (α_i) values of bluegill sunfish for larger *Daphnia magna* (see Fig. 3) as a function of the fishes' visual resolution. A large visual angle represents poor resolution. Visual angle is expressed both in minutes of arc and in milliradians.

increasing fish size, more prey will fall within the binocular field at once, perhaps facilitating prey selection. A second method by which fish might be able to estimate the size of a *Daphnia* would be to swim toward it. As the fish advances, the apparent size of the prey will increase, and it will do so more rapidly for a small prey nearby than for a large prey at a greater distance. Regan et al. (1979) reviewed several studies that show that an important piece of visual information for a variety of organisms is the rate at which retinal images grow larger. The absolute sizes of many prey items might be measured at once while a fish was swimming forward. Finally, absolute prey size might be estimated if the fish swims for a known distance in a direction other than directly at the prey. This would give it the information contained in two angles and one side of a triangle, allowing the distance to one or more prey items, and hence their absolute sizes, to be estimated (S. S. Easter, Jr., *personal communication*). We do not know if any of these mechanisms is used by fish in prey detection, and we cannot say if the bluegills used in our experiments consumed diets consistent with optimal foraging theory; however, the greater preference for large prey than predicted by the apparent size model requires us to conclude that the fish must have been able to assess absolute prey size, whatever the mechanism.

The precision of each of the three possible means of estimating true prey size just discussed, and probably any other conceivable mechanism, depends on the packing of retinal receptor cells. Fish with greater visual resolution have more cells per unit visual angle, and should be better able to assess such critical parameters of the visual environment as the number of prey in the binocular field, the rate of growth of the retinal image, or the position of the prey relative to the direction of swimming. Recently O'Brien et al. (1985) found, in binary choice experiments, that when bluegills were close to their zooplankton prey (within ≈ 10 cm for the fish sizes used), the fish tended to choose prey on the basis of absolute body size. At greater distances the fish fed according to apparent prey size. Wetterer (*personal observation*), using the model of Wetterer and Bishop (1985), and Butler and Bence (1984), using their own apparent size model, have independently reanalyzed the data from Werner and Hall (1974). Both found that at low prey densities the diets of the bluegills are well described by the apparent size model, while at high prey densities the fish showed a shift toward greater specialization on large prey. An interpretation of these results consistent with our observations is that any condition leading to poor visual resolution, whether caused by retinal anatomy, large distance to the prey, or low prey density, will cause the bluegills to feed according to apparent prey size. Conditions leading to good visual resolution permit more complex feeding behavior.

Imprecision in estimating true prey size would lead to error in choosing the optimal diet. Mittelbach (1981) and Werner et al. (1983) found that small fish were less selective and ate smaller prey on average than predicted by optimal foraging models. They pointed out that the cost of deviating from the optimal diet is much lower for small fish than it is for large fish. The effect may be compounded by the reduced visual capabilities of small fish. For these individuals, consuming the apparently largest prey may represent a simple means of assuring relatively high energy gains in comparison to expenditures (O'Brien et al. 1976) given the constraints of their visual system. As fish grow larger, their diets are more nearly optimal because they have a greater ability to estimate true prey size, and because error represents a greater energetic cost.

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